

FIRE AFFECTS ECOPHYSIOLOGY AND COMMUNITY DYNAMICS OF CENTRAL WISCONSIN OAK FOREST REGENERATION¹

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Abstract. In order to understand better the ecophysiological differences among competing species that might influence competitive interactions after, or in the absence of, fire, we examined the response to fire of four sympatric woody species found in intermediate-sized gaps in a 30-yr-old mixed-oak forest in central Wisconsin. Selected blocks in the forest were burned in April 1987 by a low-intensity controlled surface fire. The fire had significant effects during the following growing season on community structure, foliar nutrient concentrations, and photosynthesis. *Acer rubrum* seedling density declined by 70% following the fire, while percent cover increased several-fold in *Rubus allegheniensis*. In general, leaf concentrations of N, P, and K were increased by the fire in all species, although the relative enhancement decreased as the growing season progressed. Daily maximum photosynthetic rates were 30–50% higher in burned than unburned sites for *Prunus serotina*, *Quercus ellipsoidalis*, and *R. allegheniensis*, but did not differ between treatments for *A. rubrum*. Mean sunlit photosynthetic rates and leaf conductances were stimulated by the burn for all species, with the greatest enhancement in photosynthesis measured in *Q. ellipsoidalis*. Leaf gas exchange in *R. allegheniensis* was most sensitive to declining leaf water potential and elevated vapor pressure gradient, with *Q. ellipsoidalis* the least sensitive. Fire had no discernable effect on water status of these plants during a year of relatively high rainfall. In comparison with other species, *A. rubrum* seedlings responded negatively after fire—both in terms of survival/reproduction (decline in the number of individuals) and relative leaf physiological performance. Fire enhanced the abundance of *R. allegheniensis* and the potential photosynthetic performance of *R. allegheniensis*, *P. serotina*, and particularly *Q. ellipsoidalis*. We conclude that post-fire stimulation of net photosynthesis and conductance was largely the result of enhanced leaf N concentrations in these species.

Key words: *Acer*; community; competition; ecophysiology; fire; forest gap; leaf conductance; nutrients; photosynthesis; *Prunus*; *Quercus*; regeneration; *Rubus*; Wisconsin.

INTRODUCTION

A dramatic expansion of woody vegetation has occurred at the prairie–forest ecotone in North America since European settlement began in the mid-1800s (Kucera 1960, Pyne 1983, Abrams 1986). Some researchers have suggested that the forest expansion resulted from decreased fire frequency and intensity compared to that during Native American occupation (Gleason 1913, Sauer 1950, Penfound 1962, Lorimer 1983, Abrams 1985). Oak (*Quercus*) species were the primary constituents of these newly forested areas in the Midwest United States (Rice and Penfound 1959, Curtis 1959, Kucera 1960). In a further succession,

oaks are now frequently being replaced by more shade-tolerant species, perhaps also due to continued low fire frequency (Wuenschel and Valiunas 1967, Grimm 1983, Nigh et al. 1985, Abrams 1986).

Since hardwood forest fires in the upper Midwest generally have little effect on larger trees (White 1983, Abrams 1988), differential regeneration survival and seedling invasion among species probably determine successional trajectories on burned and unburned sites. However, little is known about potential ecophysiological differences among competing species that might influence competitive interactions after, or in the absence of, fire.

In other ecosystems (e.g., coniferous forest, prairie, chaparral), fire usually causes increased nutrient availability for a period of time that may vary from weeks to years depending on several factors (intensity of fire, fuel supply, climate, etc.; Raison 1979). Consequently,

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woody plants on burned plots usually have higher foliar nutrient concentrations than similar species on unburned plots, with potential ramifications for growth and allocation (James and Smith 1977, Ohmann and Grigal 1979, DeSouza et al. 1986). Shoot growth rates for resprouts on burned sites were higher than on unburned sites in chaparral (Radosevich and Conard 1980, DeSouza et al. 1986), and photosynthetic rates in several chaparral species have been observed to be greater in burned than unburned plots, especially early in the growing season (Oechel and Hastings 1983, DeSouza et al. 1986). However, due to sampling limitations, these data showing enhanced photosynthesis were presented for only one date for each of three species and for three dates in a fourth species. Thus, a sufficient data base on post-fire leaf gas exchange is not available to predict responses in midwestern hardwood forests.

In the present study, we examined the response to fire of four sympatric woody species (*Acer rubrum*, *Prunus serotina*, *Quercus ellipsoidalis*, *Rubus allegheniensis*) found in intermediate-size gaps in a 30-yr-old mixed-oak forest in central Wisconsin. The four species differ widely in their successional status. At one extreme *Rubus* is an early successional shrub that characteristically invades disturbed sites. In contrast, *Acer* is a mid-to-late-successional tree species that typically establishes abundant regeneration in the understory of dry oak forests in the Lake States (Curtis 1959). *Quercus* and *Prunus* are early-to-mid-successional species that are generally considered as intermediate between *Rubus* and *Acer* (Fowells 1965). Tree regeneration in gaps largely determines future stand structure in eastern hardwood forests under non-catastrophic conditions (Lorimer 1989), and cool surface fires are the most common fire type occurring in these forests as well as the fire type used in prescribed burning (Donaghue and Johnson 1975, Abrams 1988).

Population changes for each species were monitored following a controlled, spring surface fire, and seasonal patterns of leaf morphology, nutrient status, and physiological performance for each species were compared in adjacent burned vs. unburned plots. We hypothesized that greater foliar nutrient levels in burned plots would provide a mechanism for enhanced photosynthesis. Both field photosynthetic capacity and average "realized" photosynthesis were considered of importance in terms of interpreting photosynthetic response to post-fire conditions. Daily and seasonal patterns of net photosynthesis result from (1) maximum photosynthetic capacity, and (2) transitory conditions that cause "realized" photosynthesis to be less than the potential maximum. Therefore, the study was designed first to test whether potential post-fire changes in nutrient availability result in alterations of leaf chemistry and thus in photosynthetic capacity. Second, the study also examined the extent to which any potential enhancement of photosynthesis was realized over daily and seasonal time courses when a number of other

factors might also be limiting to photosynthesis. We also hypothesized that fast-growing shade-intolerant species such as *Rubus* would show the most positive physiological response following fire, while shade-tolerant *Acer* would show the least.

MATERIALS AND METHODS

The study was carried out at the Schmeeckle Reserve of the University of Wisconsin-Stevens Point, in Stevens Point, Wisconsin. Four blocks (0.6 to 1.4 ha) were located in a 30-yr-old hardwood stand on Plainfield soil, with half of each block randomly assigned to a burned or unburned treatment. Plainfield soil is characterized as a deep, excessively drained, medium-to-coarse sand that is medium-to-strongly acidic (Otter and Fiala 1978). For data pooled across all blocks, northern pin oak (*Q. ellipsoidalis*) represented $55 \pm 13\%$ (mean ± 1 SE) of the overstory individuals, followed in rank by red maple (*Acer rubrum*) ($12 \pm 5\%$), white oak (*Q. alba*) ($12 \pm 3\%$), paper birch (*Betula papyrifera*) ($11 \pm 6\%$), bigtooth aspen (*Populus grandidentata*) ($7 \pm 5\%$), trembling aspen (*P. tremuloides*) ($3 \pm 2\%$), and jack pine (*Pinus banksiana*), white pine (*P. strobus*) and black cherry (*Prunus serotina*) ($\leq 1\%$ each). Burn treatment plots were subjected to a surface fire on 9 April 1987. The fire began at 1030 and ended at 1200 central standard time (CST). Relative humidity and air temperature during the burn were $\approx 24\%$ and 24°C , respectively. Wind was out of the northwest at < 3 km/h. Mean flame height was < 0.3 m, and mean rate of spread for the headfire was 3.3 m/min, and we therefore considered this to be a low intensity fire.

In 1986 all trees (≥ 10 cm in diameter at breast height [dbh]) were surveyed in each of the eight half-blocks. In addition, 10 plot centers were established systematically along transects in each half-block. Centered around each of those points, seedlings (≤ 1.5 m tall) were counted, and shrub and herb cover was estimated in small (5 m^2) subplots, while saplings (> 1.5 m tall and < 10 cm dbh) were counted in larger plots (10 m^2). For purposes of this paper the term "seedling" is used for all trees ≤ 1.5 m tall, regardless of whether the stem is a true seedling, a root collar sprout, or a root sucker. Canopy cover of shrubs and herbs was estimated and grouped according to classes outlined by Daubenmire (1959). The midpoints of the six classes (2.5, 15.0, 37.5, 62.5, 85, and 97.5%) were used to compute species coverage. These surveys were made in July or August of both 1986 (pre-burn) and 1987 (post-burn). Due to high variation in population data, results are presented for all trends significant at $P < .10$.

Physiological measurements were made in the growing season after the fire. Because of the need to avoid significant defoliation of individual plants, measurements for each species were made using a population of individuals within burned vs. unburned plots. Measurements were made in only the highest light mi-

TABLE 1. Abundance of young trees and shrubs before and after a surface fire. Data are means \pm 1 SE.

A. Seedlings of clonal stems (≤ 1.5 m tall)		
	Seedlings or clonal stems (no./ha)	
	Pre-burn (1986)	Post-burn (1987)
<i>Acer rubrum</i> *	10 600 \pm 2 344	2 850 \pm 576
<i>Populus tremuloides</i> †	450 \pm 334	1 300 \pm 634
<i>Prunus serotina</i> †	28 250 \pm 14 853	18 500 \pm 9 866
<i>Quercus alba</i>	550 \pm 179	450 \pm 286
<i>Quercus ellipsoidalis</i>	2 300 \pm 304	2 450 \pm 426
B. <i>Rubus</i> and other shrubs (percent cover in 5-m ² plots)		
	Shrub cover (%)	
	Pre-burn (1986)	Post-burn (1987)
<i>Rubus allegheniensis</i> *	9.8 \pm 3.5	51.1 \pm 6.5
Other shrubs	6.5 \pm 1.0	8.1 \pm 1.6
Total shrub*	16.3 \pm 3.4	59.2 \pm 7.3

* $P < .05$, † $P < .10$ (significance of differences between abundances in the two years).

croenvironments: in intermediate-size gaps ranging from about 250 to 500 m². The most abundant woody species in these gaps were *Acer rubrum*, *Prunus serotina*, *Quercus ellipsoidalis*, and *Rubus allegheniensis*. On five days during the growing season, leaf structure and chemistry and diurnal patterns of plant water status and leaf gas exchange were measured for plants of all four species from burned and unburned plots. These plants averaged between 0.5 and 1.0 m in height and the tree species were roughly between 3 and 7 yr old. As far as was possible, we chose to make measurements on days that were relatively cloud-free and with moderate summertime temperatures, with measurement days spaced more or less regularly throughout the growing season. On one day rain showers interrupted the course of diurnal measurements.

Plant water status was measured with a pressure chamber (Ritchie and Hinckley 1975), and leaf gas exchange was measured with two units of a portable gas analyzer and cuvette system (Analytical Development Company, Ltd., Hoddesdon, England) that measures both CO₂ and water vapor exchange using a differential mass balance approach (Walters and Reich 1989). For gas exchange measurements, leaves were arbitrarily defined as "sunlit" (if receiving any direct solar irradiance) or "shaded" (if receiving no direct solar irradiance), as observed at the time of measurement. Sunlit and shaded leaves had photosynthetic photon flux densities (PPFD) $> 350 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or $< 240 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively. Maximum photosynthetic rates observed under field conditions such as those of this study are $\approx 90\%$ of those measured under optimal steady-state controlled conditions (D. S. Ellsworth and P. B. Reich, unpublished manuscript) and

thus are a useful index of potential photosynthetic capacity (Field and Mooney 1986). For this study, daily maximum net photosynthesis and leaf conductance were calculated as the average of the five highest measurements per day. A subsample of leaves was collected after gas exchange and water-status measurements for analyses of area, dry mass, and nutrient concentrations. *A. rubrum* had both relatively few leaves per plant and low numbers of seedlings in large burned gaps, so physiological sampling of this species was done less frequently and intensively than for the other three species.

Leaf areas were measured with a LI-COR Area Meter (LI-COR, Lincoln, Nebraska). Foliar nutrient concentrations were analyzed by the University of Wisconsin Soil and Plant Analysis Laboratory. Total leaf N concentrations were measured using microKjeldahl techniques, and the other nutrients were measured by inductively coupled plasma emission spectrometry. Unless otherwise noted, nutrient concentrations are expressed on a dry mass basis.

The 1987 growing season in Stevens Point, Wisconsin, was characterized by above-average temperatures and average rainfall (National Oceanic and Atmospheric Administration, personal communication). Rainfall totaled 44 cm from 1 May until 30 September, with at least 5 cm of rain received in each month.

Data were analyzed using the SAS package (SAS Institute 1985). Analyses of variance and regression analyses were primarily used, but analysis of covariance was used in analyzing photosynthetic response to treatment and species for shaded leaves, with photon flux density the covariate ($P < .001$). Multifactorial analyses of variance were used to assess response of leaf gas exchange to combined factors such as irradiance, leaf water potential, and vapor pressure gradient (VPG). In order to analyze the relationship between net photosynthesis and leaf nitrogen concentration, we pooled data from all days, but used data only from before midday for *Prunus*, *Quercus*, and *Rubus*, since, in general, afternoon photosynthetic rates were lower. Because of the limited number of total observations available for *A. rubrum*, all data were used.

RESULTS

Community data

No first-year mortality or aboveground dieback of overstory trees occurred in the burned plots. The fire top-killed (caused stem dieback) 67 to 100% of the *Prunus serotina*, *Betula papyrifera*, and *Populus grandidentata* saplings, but none of the *Q. ellipsoidalis* saplings. In the year before the fire, *P. serotina* and *A. rubrum* accounted for about 67 and 25%, respectively, of the woody seedling population. Following the fire, the seedling population in burned blocks decreased on average by ≈ 75 and 35% for *A. rubrum* and *P. serotina*, respectively (Table 1A). Numbers of *Q. ellipsoidalis* and *Q. alba* seedlings were essentially unchanged after

TABLE 2. Specific leaf mass (g/m^2 , $\bar{X} \pm 1 \text{ SE}$) of four species on 5 d in 1987. Within species there were no differences in burned vs. unburned plots, so data are pooled across these treatments. Average sample size per species per day = 32, except for day 210 ($n = 6$) and *A. rubrum* ($n = 8$).

	Day of year				
	155	181	210	217	258
<i>Acer rubrum</i>	...	40.3 ± 2.2	...	40.8 ± 4.2	47.8 ± 1.5
<i>Prunus serotina</i>	31.5 ± 1.7	39.4 ± 1.6	38.9 ± 3.2	42.1 ± 1.4	46.2 ± 1.7
<i>Quercus ellipsoidalis</i>	46.5 ± 3.6	55.3 ± 1.6	55.9 ± 2.2	55.2 ± 1.9	57.6 ± 2.0
<i>Rubus allegheniensis</i>	34.2 ± 1.3	40.0 ± 1.7	44.2 ± 3.3	44.4 ± 1.9	46.0 ± 1.7

the fire, and there was also a 200% increase in the population of *P. tremuloides* seedlings. Measurements of shrubs and herbs in 1986 and 1987 indicate an increase in *Rubus* cover (from 10 to 50%) following the fire (Table 1B). *Carex pensylvanica* cover also increased substantially after burning (data not shown).

Leaf structure and nutrient status

In general, specific leaf mass (SLM) of all species on all plots increased from the beginning to the end of the growing season (Table 2). There was no significant difference in SLM between burned and unburned plots in any species. *Quercus* always had significantly ($P < .001$) greater SLM than every other species, with no significant differences observed among the other three species.

Averaged over the growing season, foliar concentrations of several nutrients were significantly ($P < .05$) higher in burned than unburned plots for all or some species (Table 3). In *Acer* and *Prunus* foliar N and K levels were higher on burned plots, in *Rubus* N and P were higher, and in *Quercus* N, P, K, and Mg were elevated. In both burned and unburned plots *Rubus* and *Prunus* had the highest leaf N concentrations on average, with *Quercus* intermediate and *Acer* lowest. However, due to greater SLM in *Quercus*, leaf N per unit leaf area was greatest in that species, intermediate in *Prunus* and *Rubus*, and lowest in *Acer* (data not shown).

Species and treatments differed in the seasonal dynamics of leaf nutrient status, with the fire apparently producing a large pulse of available nutrients in the

period soon after the burn (Fig. 1). In early June (day 155), foliar N concentrations in *Prunus* and *Quercus* were $\approx 35\%$ greater in burned than unburned plots (Fig. 1A). During the remainder of the year, leaf N was $\approx 10\text{--}20\%$ greater in burned than unburned plots. These differences were significant ($P < .05$) for both species on all sampling dates, except for *Prunus* on day 181. In *Rubus* leaf N remained essentially unchanged over the season in unburned plots while decreasing continuously in burned plots, resulting in the following contrast: in burned plots leaf N was 50% greater on day 155, 25% greater on day 181, not significantly different on days 210 or 217, and 10% less on day 258 than in unburned plots. Differences in leaf N between burned and unburned plots also diminished over the growing season in *A. rubrum*.

In *Quercus*, increases ($P < .05$) in foliar P concentrations in burned plots were large (80–110%) and consistent over the growing season (Fig. 1B). In *Acer*, *Prunus*, and *Rubus*, stimulation of leaf P in burned plots was greatest (25–50%) early in the season, but decreased over time, and by September no differences in leaf P remained between burned and unburned plots. In all four species, leaf K concentrations were higher in burned than unburned plots early in the growing season (data not shown). In *Acer*, *Quercus*, and *Prunus* these differences disappeared by the end of the season, while in *Rubus* leaf K concentrations became lower in burned than unburned plots by that time. Since SLM did not differ significantly among plants in burned and unburned plots, the above patterns hold for nutrient concentrations expressed on an area or dry mass basis.

TABLE 3. Nutrient concentrations (mean % dry mass) pooled across the growing season for four species in burned and unburned plots in central Wisconsin. Data were equally weighted for days 155, 181, 217, and 258, except for *A. rubrum*, for which no data were available on day 155. Values within a column with the same superscript letter are not significantly different ($P < .05$, Tukey's studentized range test).

		N	P	K	Ca	Mg
<i>Acer rubrum</i>	Burned	2.02 ^c	0.11 ^{cd}	0.58 ^c	0.83 ^{ab}	0.26 ^c
	Unburned	1.73 ^d	0.10 ^{cd}	0.47 ^d	0.91 ^a	0.25 ^c
<i>Prunus serotina</i>	Burned	2.87 ^a	0.14 ^{bc}	0.91 ^a	0.76 ^{ab}	0.37 ^b
	Unburned	2.44 ^b	0.12 ^{bcd}	0.68 ^{bd}	0.79 ^{ab}	0.38 ^b
<i>Quercus ellipsoidalis</i>	Burned	2.51 ^b	0.18 ^a	0.70 ^b	0.52 ^c	0.24 ^c
	Unburned	2.09 ^c	0.09 ^d	0.59 ^c	0.59 ^c	0.18 ^d
<i>Rubus allegheniensis</i>	Burned	2.74 ^a	0.21 ^a	0.76 ^{ab}	0.72 ^b	0.45 ^a
	Unburned	2.41 ^b	0.13 ^{bc}	0.82 ^{ab}	0.67 ^{bc}	0.51 ^a
Range of SE		0.03–0.09	0.01–0.02	0.03–0.08	0.02–0.09	0.01–0.03

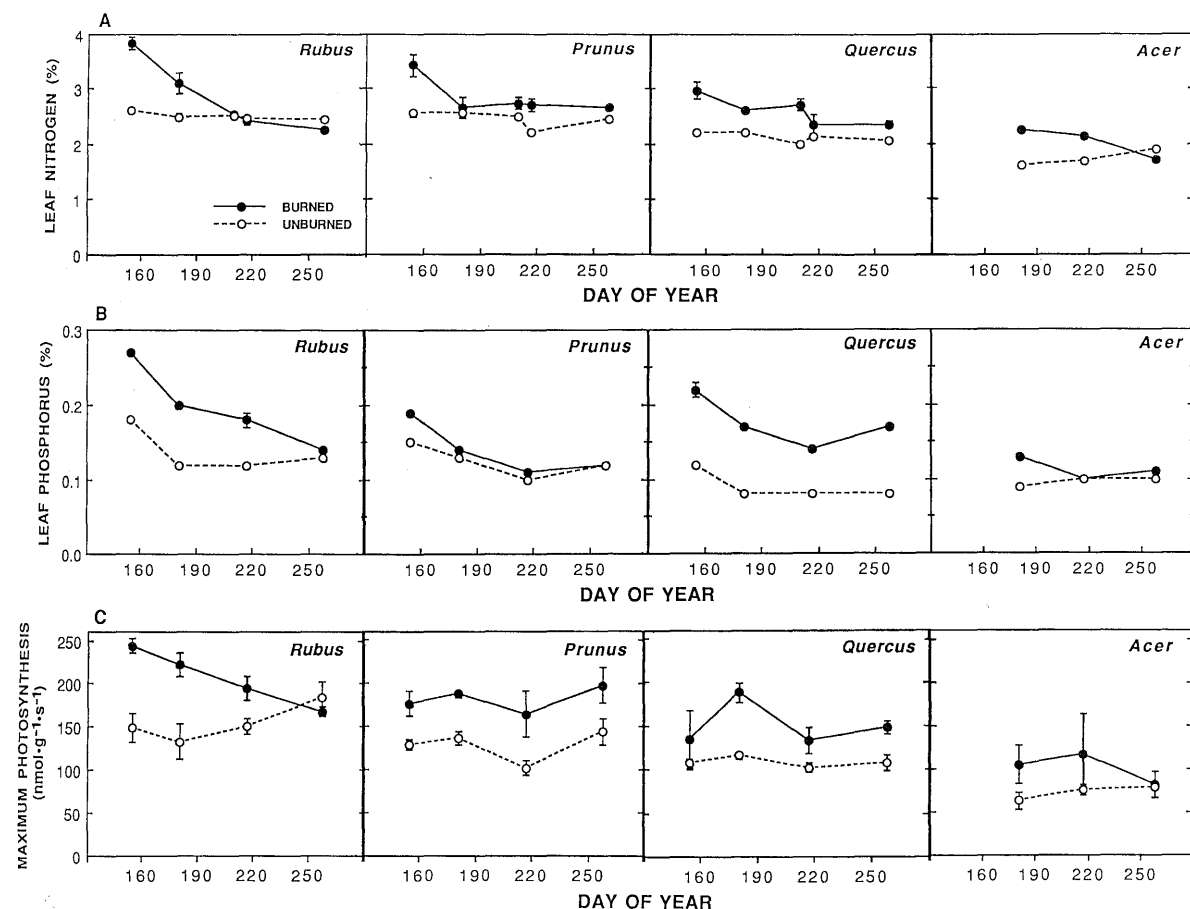


FIG. 1. Seasonal variation (means \pm 1 SE) in leaf nutrient concentrations and maximum mass-based net photosynthesis for four species on burned (●) and unburned (○) forest gaps in central Wisconsin. (A) Nitrogen; (B) Phosphorus; (C) Net photosynthesis.

Soil moisture and plant water status

Due to relatively abundant rainfall during the growing season, soil moisture was generally high throughout the summer, as indicated by high soil water content (data not shown) and high pre-dawn water potential in all species measured (Fig. 2). There were no significant differences in pre-dawn water potential between indi-

viduals on burned vs. unburned plots, or between species.

Daytime minimum leaf water potentials did not consistently differ for any species in burned vs. unburned treatments (Fig. 2). Early in the season there were no significant differences among species in minimum daily water potential, but on the last two sampling dates water potential in *Quercus* was significantly lower than

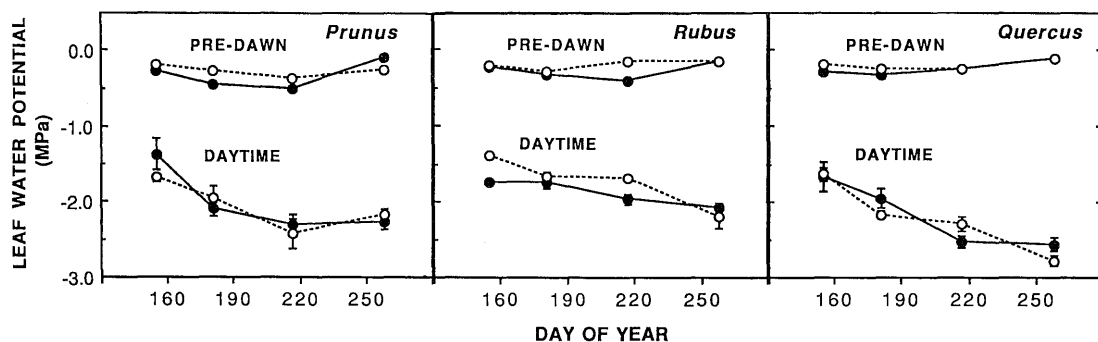


FIG. 2. Seasonal variation (means \pm 1 SE) in pre-dawn and mean minimum daytime leaf water potential for three species on burned (●) and unburned (○) forest gaps in central Wisconsin.

TABLE 4. Three measures of net photosynthesis and leaf conductance for four species on burned and unburned plots in central Wisconsin pooled over all sampling dates (means \pm 1 SE). Daily maximum rates averaged for the five highest observations per day. Values within a column with the same superscript letters are not significantly different ($P < .05$, Tukey's studentized range test).

Species	Treatment	Daily maximum		Mean sunlit		Mean shaded	
		Photo-synthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Photo-synthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Photo-synthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
<i>Acer rubrum</i>	Burned	3.8 \pm 0.2 ^e	166 \pm 41 ^e	3.5 \pm 0.2 ^d	147 \pm 10 ^e	1.1 \pm 0.2 ^a	123 \pm 12 ^c
	Unburned	4.0 \pm 0.2 ^e	149 \pm 52 ^e	3.0 \pm 0.2 ^c	116 \pm 7 ^f	0.9 \pm 0.2 ^a	121 \pm 10 ^c
<i>Prunus serotina</i>	Burned	8.0 \pm 0.4 ^{bc}	430 \pm 71 ^{bc}	5.8 \pm 0.3 ^a	296 \pm 19 ^b	1.0 \pm 0.1 ^a	166 \pm 10 ^b
	Unburned	5.9 \pm 0.4 ^d	263 \pm 60 ^{de}	4.4 \pm 0.2 ^{bc}	163 \pm 10 ^{dc}	1.1 \pm 0.1 ^a	131 \pm 9 ^c
<i>Quercus ellipsoidalis</i>	Burned	9.0 \pm 0.3 ^{ab}	446 \pm 48 ^b	6.3 \pm 0.3 ^a	298 \pm 22 ^b	1.0 \pm 0.1 ^a	167 \pm 12 ^b
	Unburned	5.7 \pm 0.4 ^d	282 \pm 51 ^{cde}	3.9 \pm 0.2 ^{cd}	183 \pm 11 ^d	0.9 \pm 0.1 ^a	127 \pm 11 ^c
<i>Rubus allegheniensis</i>	Burned	9.3 \pm 0.4 ^a	805 \pm 91 ^a	5.8 \pm 0.3 ^a	401 \pm 32 ^a	0.5 \pm 0.1 ^b	252 \pm 14 ^a
	Unburned	6.4 \pm 0.4 ^{cd}	381 \pm 47 ^{bcd}	4.5 \pm 0.2 ^b	249 \pm 15 ^c	1.0 \pm 0.1 ^a	185 \pm 14 ^b

in either *Rubus* or *Acer*. Daytime minimum leaf water potential decreased ($P < .05$) for all species on burned and unburned plots from early to late season.

Gas exchange

Rates of net photosynthesis pooled from all days and all times of day for sunlit leaves (PPFD $> 350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were significantly greater ($P < .01$) in burned than unburned plots for all species (Table 4). There was also a significant interaction ($P < .05$) between species and treatment (burn vs. no burn), indicating a differential ability among species to respond to post-fire conditions. *Quercus* had the greatest fire-induced relative and absolute stimulation of mean photosynthesis (60% and $2.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), followed by both *Prunus* and *Rubus* ($\approx 30\%$ and $1.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and *Acer* (15% and $0.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Using the more limited amount of data available for mass-based rather than area-based photosynthesis, results of all analyses were similar (data not shown).

There were significant differences in mean sunlit leaf conductance values between treatments and species, but there was no significant interaction (Table 4). In all species, plants on burned plots had higher mean leaf conductances than on unburned plots. Leaf conductance was significantly greater in *Rubus* than in all other species, with *Prunus* and *Quercus* also having significantly greater conductance than *Acer*. Increases in conductance on burned plots were 80% in *Prunus*, 60% in *Quercus* and *Rubus*, and 30% in *Acer*. For *Acer*, *Prunus*, and *Rubus* the relative percent stimulation in mean leaf conductance on burned plots was twice as great as the stimulation in photosynthesis, while increases in the two parameters were similar for *Quercus*. In all species, transpiration rates at all times of day were significantly higher for plants on burned than unburned plots (data not shown), despite no differences in leaf water potential. This suggests that soil-to-leaf hydraulic conductance was greater in burned than unburned plants.

Significant species and treatment effects were observed for gas exchange rates of "shaded" leaves as well. Mean values of photosynthetic photon flux density (PPFD) for shaded leaves used in gas exchange measurements were not significantly different among treatments or species. Net photosynthetic rates were significantly lower for shaded *Rubus* leaves on burned plots than for any other species-treatment combination (Table 4). For conductance of shaded leaves, all species but *Acer* had higher rates on burned than unburned plots. *Rubus* had higher conductance in shaded leaves than the other species, with *Acer* significantly lower than *Prunus* and *Quercus* on the burned plots.

Daily maximum net photosynthesis and leaf conductance, averaged among sampling dates, were significantly ($P < .05$) higher on burned than unburned plots for *Quercus*, *Prunus*, and *Rubus*, but not *Acer* (Table 4). In *Quercus* and *Rubus* on burned plots, the stimulation of maximum photosynthesis was almost 50% compared to unburned plots, with stimulation of 30% for *Prunus* and 0% for *Acer*, respectively. Among species in both burned and unburned plots, maximum photosynthesis and leaf conductance were least in *Acer*. Daily maximum photosynthesis in *Rubus* was not significantly higher than in *Quercus*, while maximum leaf conductance was 40–75% higher in *Rubus*, suggesting lower water use efficiency in *Rubus* than in *Quercus* under optimal field conditions.

At all times of day in *Prunus*, *Quercus*, and *Rubus*, average rates of leaf conductance and photosynthesis for sunlit leaves were higher in burned than unburned plots, although differences tended to be greatest early in the day, especially for *Prunus* and *Rubus* (Fig. 3). In *Acer*, there was a trend for gas exchange rates to be higher around midday in burned than unburned plots, otherwise there were no differences. In *Prunus* and *Rubus* gas exchange rates were highest in the morning and generally declined throughout the day, with this pattern being displayed least by *Quercus*.

Within each species there was no significant difference between the leaf N and net photosynthesis rela-

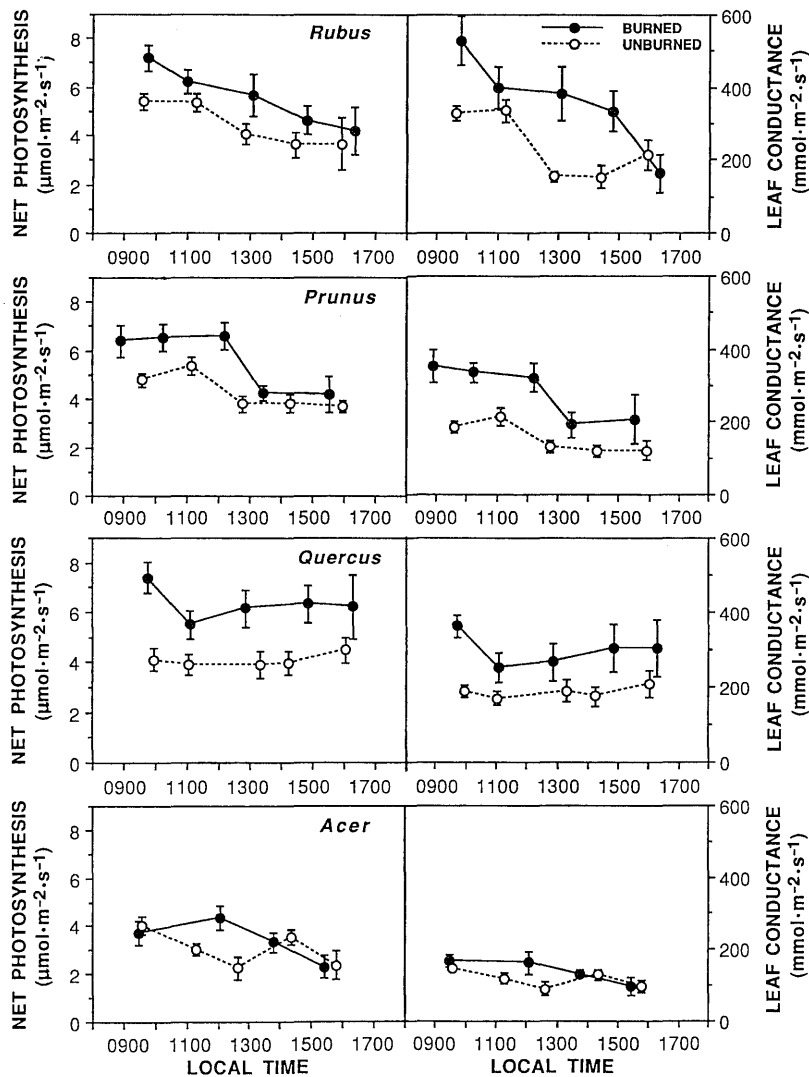


FIG. 3. Mean (± 1 SE) diurnal patterns of gas exchange of sunlit leaves for four species on burned (●) and unburned (○) forest gaps in central Wisconsin. Time in United States central daylight savings time.

tionship for data from burned and unburned plots, so data from both treatments were pooled for presentation herein. For each species, there was a significant linear relationship between leaf N and net photosynthesis with both expressed on an area basis (Table 5). The slope of the relationship was steepest in *Quercus*, followed in order by *Prunus*, *Rubus*, and *Acer*. The relationship between leaf N and net photosynthesis was

generally poorer or not significant when both N and photosynthesis were expressed on a dry-mass basis (data not shown).

Since leaf N was higher on burned than unburned plots (Table 3) and had similar positive effects on net photosynthetic rates in all plots (Table 5), we conclude that the post-fire stimulation of net photosynthesis was largely a result of enhanced leaf N concentrations. Sev-

TABLE 5. Relationship between net area-based photosynthesis (P_s , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and leaf nitrogen (N_{area} , g/m^2) for four species in forest gaps in central Wisconsin. Since there were no significant differences within species in this relationship between burned and unburned plots, data are pooled within species in statistical analyses.

	Regression equations	<i>P</i>	<i>r</i> ²
<i>Acer rubrum</i>	$P_s = 0.6 + 3.41(N_{\text{area}})$	<.05	0.30
<i>Prunus serotina</i>	$P_s = 1.6 + 4.13(N_{\text{area}})$	<.001	0.41
<i>Quercus ellipsoidalis</i>	$P_s = -1.1 + 5.36(N_{\text{area}})$	<.001	0.54
<i>Rubus allegheniensis</i>	$P_s = 2.6 + 3.80(N_{\text{area}})$	<.01	0.27

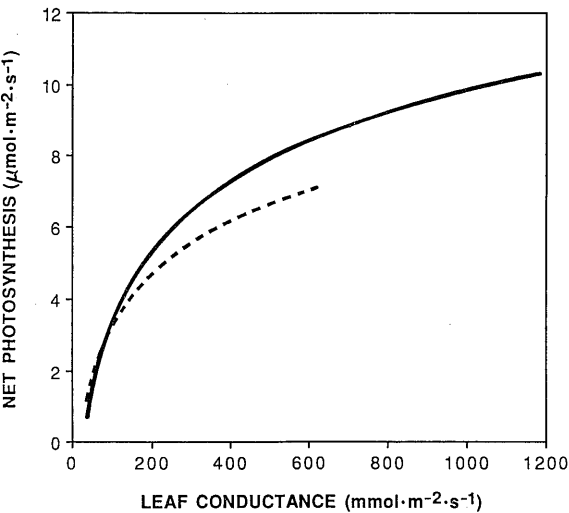


FIG. 4. Relationship between net photosynthesis (P_s) and leaf conductance (g) for leaves on burned (—) and unburned (---) sites. Regressions are derived from all sunlit data obtained before 1300. There was no species \times treatment interaction upon the photosynthesis vs. conductance relationship; hence, data for all species are pooled within treatments. Equation for unburned sites is $P_s = -6.54 + 2.13 (\ln g)$, $r^2 = 0.58$, $P < .0001$. Equation for burned sites is $P_s = -9.52 + 2.80 (\ln g)$, $r^2 = 0.52$, $P < .0001$. The difference in slope between the two equations is significant at $P = .01$.

eral other lines of evidence support this idea. Inasmuch as mass-based leaf N concentration appears to largely determine maximum mass-based photosynthesis among and within species (Field and Mooney 1986), we ask whether seasonal patterns in maximum mass-based net photosynthesis in burned vs. unburned plots were similar to those for leaf N concentration. The results (Fig. 1) appear to largely support this contention: *Quercus* and *Prunus* exhibited higher photosynthesis and leaf N in burned plots throughout the season, while *Acer* and *Rubus* exhibited higher photosynthesis and leaf N in burned plots early in the season, with differences between burned and unburned plots disappearing over time. Plants on burned plots also had greater net photosynthetic rates for a given level of leaf conductance than those on unburned plots (Fig. 4).

There was no interaction between species and treatment on this relationship. Greater net photosynthesis for a given level of leaf conductance likely results from greater biochemical carbon dioxide fixation capacity, which is related to concentrations of nitrogenous compounds such as RuBP carboxylase (Field and Mooney 1986).

Both vapor pressure gradient (VPG) and leaf water potential appeared to limit gas exchange in sunlit leaves. There were no mean differences among species or treatments in microenvironment (e.g., VPG) for the gas exchange data set. Response of leaf gas exchange to leaf water potential or VPG did not differ among burned and unburned plots, so data were pooled by species. Both *Rubus* and *Prunus* showed a significant ($P < .01$) linear decrease in leaf conductance as a function of declining leaf water potential, with a steeper slope for *Rubus* than for *Prunus* (Table 6). Conductance in *Quercus* and *Acer* was not significantly affected by leaf water potential. *Rubus* had a significant ($P < .01$) negative response of area-based photosynthesis to declining water potential, but the other three species did not (Table 6).

Leaf gas exchange rates were negatively correlated with increasing VPG in all species (Table 6). The slopes of these responses were greatest in *Rubus* and least in *Quercus* and *Prunus*. Since VPG and leaf water potential are usually highly correlated, it is not possible from these analyses to determine whether leaves were directly responding to VPG, water status, or both. However, for *Quercus*, and to a lesser extent *Prunus* and *Acer*, significant responses to VPG were observed at levels of leaf water potential that apparently did not cause stomatal response.

DISCUSSION

A surface fire in early spring had significant effects during the following growing season on community composition and ecophysiology of regeneration in a central Wisconsin hardwood forest. The effects of fire on seedling ecophysiology were a result of changes in nutrient availability and/or root-shoot balance. Important differences in ecophysiological response among species were observed as well, perhaps related to differences in their successional status. The effects of fire

TABLE 6. Relationships between leaf conductance (g) and net photosynthesis (P_s) and either leaf water potential (ψ) or vapor pressure gradient (VPG). Data are pooled from burned and unburned plots, since no differences in response were observed between these groups. Significant relationships are noted by ** $P < .01$ and * $P < .05$. Units: g : ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); P_s : ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); ψ : (MPa); VPG: (kPa). All data are for sunlit leaves (photosynthetic photon flux density $> 350 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

	g and Ps as a function of leaf water potential (ψ)		g and Ps as a function of vapor pressure gradient (VPG)	
	g	Ps	g	Ps
<i>Acer rubrum</i>	NS	NS	NS	$P_s = 5.7 - 1.8\text{VPG}^*$
<i>Prunus serotina</i>	$g = 455 + 112\psi^{**}$	NS	$g = 366 - 87.6\text{VPG}^*$	$P_s = 6.5 - 1.1\text{VPG}^*$
<i>Quercus ellipsoidal</i>	NS	NS	$g = 368 - 87.9\text{VPG}^*$	$P_s = 7.3 - 1.4\text{VPG}^*$
<i>Rubus allegheniensis</i>	$g = 759 + 252\psi^{**}$	$P_s = 9.57 + 2.6\psi^{**}$	$g = 571 - 160.8\text{VPG}^{**}$	$P_s = 8.6 - 2.3\text{VPG}^{**}$

on community composition were primarily due to differential mortality and reproduction between species.

In terms of nutrient cycling processes, many basic cations (e.g., P, K, Ca, Mg, and Na) are released when the vegetation and surface organic layer are consumed by fire, and therefore increase in the soil (Ahlgren and Ahlgren 1960). The situation with N is more complex because it is easily volatilized during fire. There is increasing evidence, however, that microbial N fixation and transformation (mineralization) are stimulated by post-fire conditions (e.g., increased soil moisture, soil temperature, nutrient availability, and pH), which may increase soil N availability (cf. Christensen 1973, St. John and Rundel 1976). An increase in soil nutrients often increases certain foliar nutrients in the post-burn vegetation. Following the 1971 Little Sioux fire in Minnesota, P, Ca, and Mg concentrations were higher in vegetation from burned than unburned stands (Ohmann and Grigal 1979). In southern Ontario, N, P, K, Ca, and Mg were 24–42% higher in trembling aspen leaves on burned compared to unburned areas (James and Smith 1977). Forest shrubs in burned larch–Douglas-fir forests in Montana had significantly higher concentrations of N, P, Na, Fe, and Mn than shrubs in the unburned controls (Stark and Steele 1977).

Similar results were observed in our Wisconsin study. In general, leaf concentrations of N, P, and K were increased in all study species by the fire, although this enhancement tended to decrease as the growing season progressed. This could be explained by a limited period of increased nutrient availability in the rooting zone after fire, or a growth stimulation that in essence diluted the nutrients within a greater amount of plant tissue, or both. An initial pulse followed by a decrease in nutrient levels in foliage and surface soil with time after fire has been previously reported (Christensen 1977, Covington and Sackett 1984, Knapp 1985).

Mineral nutrition often has a pronounced effect on leaf physiological function. Studies involving a wide variety of plant species have demonstrated a positive relationship between N concentrations in leaves and gas exchange rates (Longstreth and Nobel 1980, Gulmon and Chu 1981, Field and Mooney 1986). Moreover, low concentrations of leaf P, K, and Mg have also been correlated with low photosynthetic rates (Longstreth and Nobel 1980, Rao et al. 1987, Reich and Schoettle 1988). In the present study, field photosynthetic capacity (defined as maximum observed values) and maximum leaf conductance were significantly increased in burned plots for all species except *Acer*. Since burned and unburned plants did not differ in their leaf N : photosynthesis relationships, we attribute much of the gain in field photosynthetic capacity in burned plants directly to elevated leaf N concentrations (Field and Mooney 1986). Differences between burned and unburned plants in seasonal patterns of leaf N and photosynthesis and in photosynthesis : leaf conductance relationships also support this

view. Increased soil-to-leaf hydraulic conductance may also contribute to increased photosynthesis if leaf conductance increases along with hydraulic conductance (Reich and Hinckley 1989). Post-fire vegetation in chaparral and prairie ecosystems has increased leaf gas exchange rates relative to unburned vegetation, and this has been attributed as well to fire-induced improvements in nutrient status and water relations (Oechel and Hastings 1983, Knapp 1985, DeSouza et al. 1986).

As mentioned earlier (*Results: Gas exchange*), both maximum potential photosynthesis (as above) and the lower rates “realized” over the course of the day should be considered in evaluating field photosynthetic performance. All four species tended to have maximum gas exchange rates in the morning (Fig. 3), with rates declining more or less throughout the day. Mean photosynthetic rates and leaf conductances (for sunlit leaves) were greater in the burned plots for all species, with *Quercus* showing a significantly greater enhancement of photosynthesis than the other species. It is interesting that *Acer* had significantly higher average net photosynthesis and leaf conductance on burned than unburned plots, despite not having an increase in maximum photosynthesis or leaf conductance. This was apparently a result of *A. rubrum* on burned plots maintaining relatively high gas exchange rates during midday (Fig. 3), when unburned *A. rubrum* plants were experiencing depressions in gas exchange rates typically associated with midday water stress (Hinckley et al. 1978). For all four species, the results suggest that enhanced photosynthetic capacity and/or the maintenance of relatively high photosynthetic rates throughout the day should contribute to greater carbon gain in leaves of burned than unburned plants. If increases in mean daily carbon gain were similar in relative magnitude to increases in mean photosynthetic rates (15–60%), this would be an important contribution to plant carbon balance.

Within species, photosynthesis–leaf N relationships in this study were stronger on area than on mass bases. This is in contrast to the data of Field and Mooney (1986) among species largely from high-light environments, but agrees with recent results from our laboratory for temperate and tropical species in shaded or partially shaded environments (D. S. Ellsworth and P. B. Reich, *unpublished manuscript*; P. B. Reich, M. Walters, D. S. Ellsworth, and C. Uhl, *unpublished manuscript*). In understory or gap environments, light-harvesting may be an important competitive feature, and thus area-based photosynthetic potential may be more important, and more tightly coupled with N, than mass-based photosynthetic potentials in such environments.

Stimulation of photosynthesis and leaf conductance in burned plots probably resulted largely from greater foliar N concentrations, but altered root–shoot dynamics should be considered as well. Most of the seedlings in the burned gaps in this study were top-killed by the

fire, with the result that the vast majority of above-ground stems in burned plots were 1987 sprouts, while those in unburned plots were largely original stems, or sprouts from previous years or from 1987. Comparisons of leaf function between young northern red oaks (*Q. rubra*) that were stem-pruned and those that were not (Kruger and Reich 1989, E. L. Kruger and P. B. Reich, *unpublished manuscript*) show certain similarities to differences between the burned and unburned individuals in this study. Pruned individuals had higher photosynthetic rates and leaf conductances than unpruned red oak plants, yet they had similar water deficits. The enhanced photosynthesis of pruned red oak appeared to be a result of alteration in root : leaf source/sink relations. The similarities between the results of the two studies suggest that altered root : shoot relations following top-kill probably contributed partially to some of the differences observed between burned and unburned plants in this study.

Can changes in foliar nutrient concentrations also be attributed to changes in root : shoot dynamics? Although pruned red oak plants did have a minimal increase in leaf nutrient concentration in contrast to unpruned plants (E. L. Kruger and P. B. Reich, *unpublished manuscript*), the increase was considerably less than the differences observed between burned and unburned plants in this study. Also, the seasonal timing of burned vs. unburned plot nutritional differences (Fig. 1) and prior documented evidence for post-fire nutrient pulses (e.g., Christensen 1977, Knapp 1985) suggest that most of the increase in leaf nutrient concentration observed in this study resulted from effects of fire on nutrient availability, rather than on altered root : shoot relations due to top-killing of plants by the fire.

Fire had minimal effect on water status of the plants during the study year. However, 1987 was a relatively rainy summer and significant, pre-dawn, plant water deficits did not occur. In a dry summer, such as in the following year 1988, when pre-dawn water deficits throughout Wisconsin were often -1 to -2 MPa lower than in 1987 (D. S. Ellsworth, E. L. Kruger, and P. B. Reich, *personal observation*), potential differences due to treatments and species could be important. Under drought conditions, differences in root : shoot allocation and hence in soil-to-leaf hydraulic conductance between burned and unburned plots might be important in terms of development of significant, pre-dawn, plant water stress. The "water-spending" strategy of *Rubus* may be advantageous during years when rainfall is plentiful, such as the study year, but its drought sensitivity may prove disadvantageous during dry years or on more xeric sites.

At the community level, *Rubus* had a positive response to fire and abundance of *Acer* and *Prunus* seedlings a negative response, with abundance of *Quercus* seedlings unaffected. Differential mortality, sprouting ability, and rates of revegetation were likely responsible for these differences. Stems of *Quercus* saplings were

uniformly resistant to the fire, but heavy aboveground dieback was observed in saplings of other species. Leaf and whole-plant physiological response also differed among species. Elevation of foliar N, P, and K was briefest in *Rubus* and longest in *Quercus*, especially for P. The increased leaf nutrient levels and altered root : shoot relations of seedlings on burned plots resulted in increased average photosynthetic rates for sunlit leaves in all species. However, this response was significantly greater in oak than in the other species. This may have resulted from a steeper response of photosynthesis to increasing leaf N in oak and to greater tolerance of VPG and plant water deficits in this species. *Prunus* and *Rubus* in particular were sensitive to VPG and leaf water potential, and under conditions of high VPG or low water status these species were not able to maintain high photosynthetic rates. Thus, interactions with other stresses appear to temporally limit the ability of individual *Prunus* and *Rubus* plants to photosynthetically profit from post-burn conditions, in comparison with *Quercus*.

How can one assess the relative ecological importance of fire-induced changes in individual plant performance vs. changes in populations of seedlings/sprouts? Strength of statistical significance may not be representative of relative biological significance (Anonymous reviewer of this paper, *personal communication*). For instance, the statistical significance of changes in net photosynthesis was greater than for changes in population or cover. However, fire-induced changes in net photosynthesis ranged from 15 to 60% in the four species, while changes in population or cover ranged from -70% in *A. rubrum* to $+400\%$ in *R. allegheniensis*. Given the current data set and the experimental design, it is impossible to determine whether changes in populations or in performance of individuals will have more impact on woody plant dynamics following fire in these forest habitats (or in what ways they might interact). However, the results of this study do suggest that both may have significant influence on woody plants in such systems.

In summary, many of the differences among species observed in this study were consistent with their purported differences in successional status, fire resistance, and performance on disturbed sites. Taken as a whole, *Acer*, a later successional species, responded most negatively following fire, both in terms of survival/reproduction (decline in the number of individuals) and in relative leaf physiological performance of seedlings/sprouts in a comparative sense. Numbers of *Rubus* stems responded most positively to the post-burn gap environment, whereas the number of stems of *Prunus* declined somewhat, and *Quercus* remained unchanged. Characteristic of being the most opportunistic and early successional species studied, *Rubus* maintained greater leaf conductance than the other species, but it was also most sensitive to decrease in leaf water potential and increased VPG. *Quercus*, considered the

most fire and drought resistant of the species, exhibited greater daily maximum and mean net photosynthesis on burned vs. unburned sites and was the least sensitive species to decreases in water status. *Prunus* was intermediate among the species in terms of survival and physiological function following fire.

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